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# Anatomy of the Circulatory System of the Nudibranch *Platydoris argo* (Linné, 1767) with Comparisons among Doridacea (Gastropoda: Opisthobranchia)

by

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*Abstract.* The anatomy of the circulatory system of *Platydoris argo* (Linné, 1767) is described. The morphology of the heart and the placement of its valves are studied in detail. The auriculoventricular and aortic valves may prevent a backward blood flow. Blood coming from the branchial ring enters the auricle through the caudomedial opening, while the blood that comes from the lateral sinuses goes into the auricle through the lateral openings. The distribution of the arterial system throughout the animal's body is described. Following this, the variability of the circulatory system in Doridacea is compared and discussed, showing the changes in the heart, gills, and main blood vessels within the suborder.

## INTRODUCTION

The circulatory system of the Nudibranchia has been studied little. Detailed studies on Doridacea are few, even though they have varied anatomical features (POTTS, 1981; WÄGELE, 1984; JONAS, 1985). Thus, the gills of dorids can be located on the notum or around the anus, or they can be disposed along both sides between the notum and the foot. In addition, the stage of complexity in the development of the gills differs within the suborder. The range of forms includes some leaflets or simply pinnate gills, not retractile, as well as complex tripinnate gills retractile within a branchial pocket. According to variations of the respiratory structures, the vascular system also shows modifications in the afferent and efferent branchial vessels.

The present work describes in detail the circulatory system of a cryptobranchiate dorid and compares it to that of other doridacean mollusks.

## MATERIALS AND METHODS

The seven specimens of *Platydoris argo* (Linné, 1767) used for this study were collected in the Strait of Gibraltar (southern Spain) and measured between 6 and 10 cm in length. Four of these animals, collected in August 1985, had been preserved in 4–5% formalin. The other three specimens, obtained in October 1988, were anesthetized with magnesium chloride before preservation in formalin, in order to keep their gills extended for anatomical investigations.

Dissections were made with fine forceps and needles using a stereomicroscope. Details of vessels and sinuses were observed by sectioning the notum of the specimens that were preserved in formalin and staining them with methylene blue. In the anesthetized specimens, a bubble of air was injected into the ventricle and main arteries, allowing us to follow the blood stream throughout the body.

## RESULTS

### Pericardium

The pericardium is a spacious cavity lying posteriorly on the digestive gland in front of the branchial circle (Figure 1). Associated with the pericardial cavity are the following vessels: (*a*) the aortic trunk (Figure 3, at), which is the beginning of the arterial system and is located just anterior to the pericardium; (*b*) the branchiocardiac vein (bv), which is located at the posterior extreme of the pericardium and connects the afferent branchial ring to the auricle; and (*c*) the auricular veins (av), which connect the lateral sinuses to the side of the auricle. The circular sinus

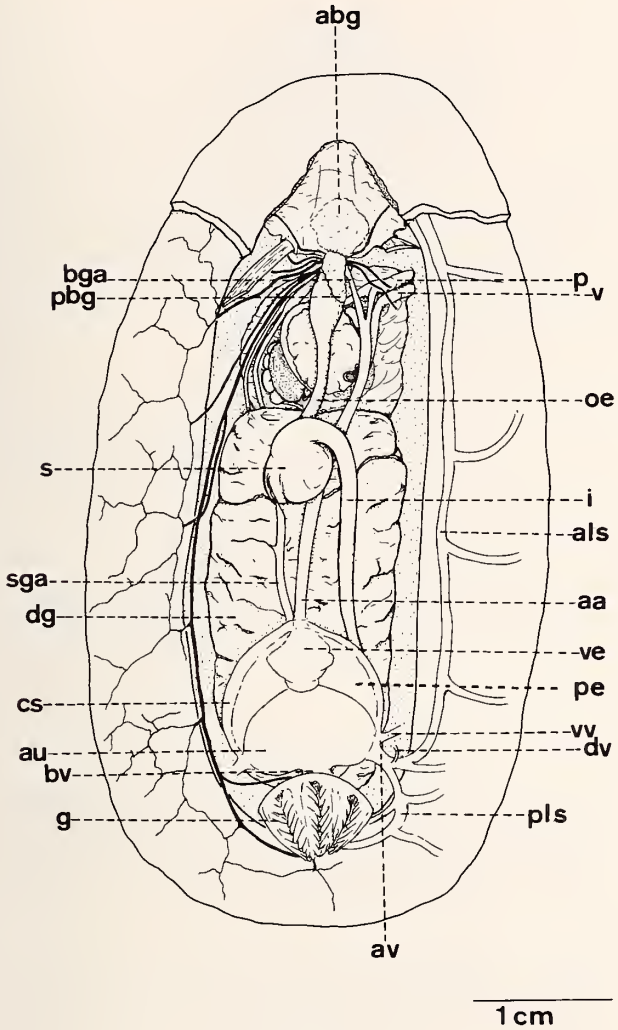


Figure 1

Dorsal view of a dissected *Platydoris argo*. aa, anterior artery; abg, anterior blood gland; als, anterior lateral sinus; au, auricle; av, auricular vein; bga, blood gland artery; bv, branchiocardiac vein; cs, circular sinus; dg, digestive gland; dv, dorsal vein; g, gill; i, intestine; oe, oesophagus; p, penis; pbg, posterior blood gland; pe, pericardium; pls, posterior lateral sinus; s, stomach; sga, superior gastric artery; v, vagina; ve, ventricle; vv, ventral vein.

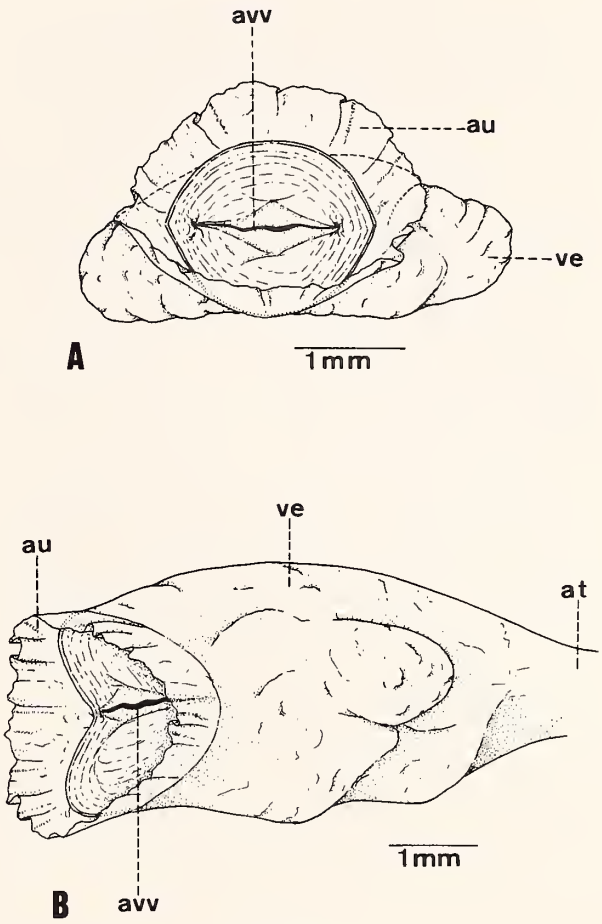


Figure 2

Posterior (A) and lateral (B) view of the ventricle of *Platydoris argo*. at, aortic trunk; au, auricle; avv, auriculoventricular valve; ve, ventricle.

(cs) is a spacious inner cavity that encircles all but the posterior end of the pericardium. The only connection between this sinus and other structures is through the auricular vein, which connects to the auricle.

The heart lies within the pericardial cavity and has a rhomboid-shaped muscular ventricle and a thin-walled, globular-shaped auricle. Blood flows from the gills to the auricle through the branchiocardiac vein. The auricle also receives blood through the lateral auricular veins from a plexus of sinuses. These sinuses, which extend throughout the notum, are the sites of cutaneus respiration.

There are two valves in the heart: the auriculoventricular valve (Figure 2, avv) that has two flaps projecting into the cavity of the ventricle from the auricle, and the aortic valve (Figure 3, aov) that has a ventral flap between the ventricle and the aortic trunk.

## Peripheral Circulation

The peripheral circulation (Figure 1) consists of a plexus of sinuses that extend throughout the notum and foot of the animal. These sinuses drain laterally into two pairs of longitudinal sinuses—the anterior (als) and posterior lateral sinuses (pls)—located along the sides of the body. The anterior lateral sinus extends longitudinally up to the posterior lateral extreme of the pericardial cavity, receiving blood mainly from the lateral notum and draining it into the auricular veins. The posterior lateral sinus extends from the posterior extreme of the animal to the pericardial cavity; it carries blood from the portion of the notum located behind the pericardium and the auricular veins. The auricular veins receive blood from the dorsal notum sinuses

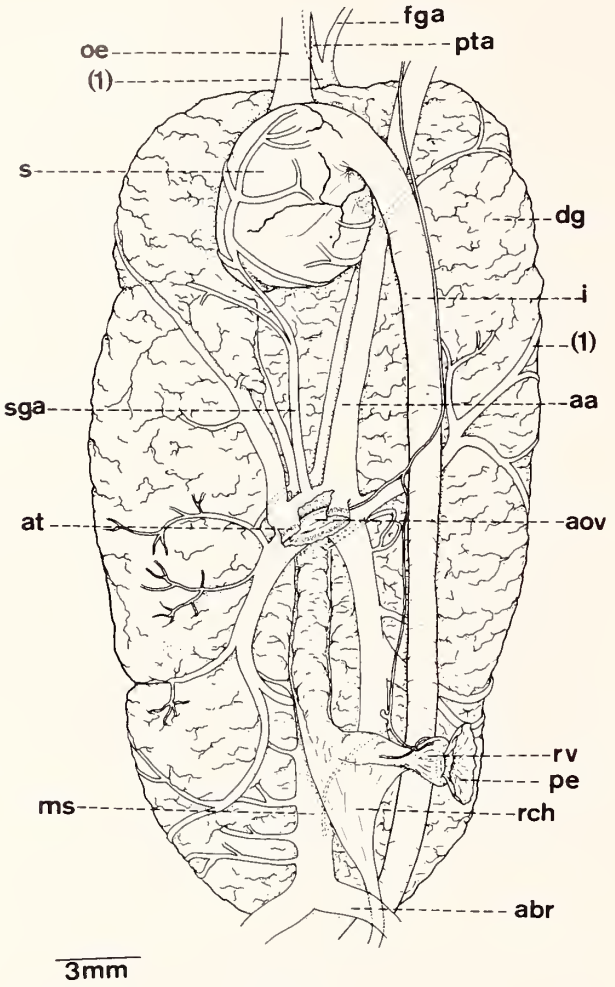


Figure 3

Dorsal view of the gonohepatic mass and stomach of *Platydoris argo* to show the arterial and venous systems. aa, anterior artery; abr, afferent branchial ring; aov, aortic valve; at, aortic trunk; dg, digestive gland; fga, female gland artery; i, intestine; ms, medial sinus; oe, oesophagus; pe, pericardium; pta, prostatic artery; rch, renal chamber; rv, renal vesicle; s, stomach; sga, superior gastric artery; (1), artery to prostate and female gland.

through the dorsal vein (dv). Blood flows from the ventral sinuses to the circular sinus through the ventral vein (vv).

## Branchial Circulation

Blood from the visceral organs is drained into a common medial sinus (Figure 3, ms) that extends along the digestive gland and under the pericardium. This sinus connects posteriorly to the afferent branchial ring (abr), which lies beneath the branchial tuft that partially encircles the anal and renal orifices. Blood passes from the afferent branchial ring into the afferent branchial vessels (Figure 4, abv), which extend longitudinally along the inner edges of the gills. These veins ramify into several small vessels that

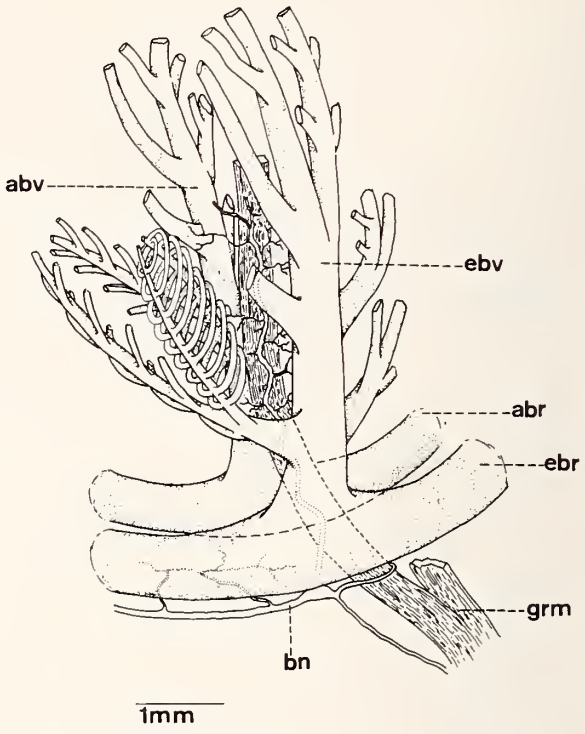


Figure 4

Partial lateral view of the branchial vessels and the afferent and efferent rings of *Platydoris argo*. abr, afferent branchial ring; abv, afferent branchial vessel; bn, branchial nerves; ebr, efferent branchial ring; ebv, efferent branchial vessel; grm, gill retractor muscle.

extend into the gill pinnules. Blood passes from the afferent branchial vessels to the efferent branchial vessels (ebv). These lie on the outer surface of the gills and join the efferent branchial ring (ebr), which lies ventral to the gill tuft and encircles the afferent branchial ring. The efferent

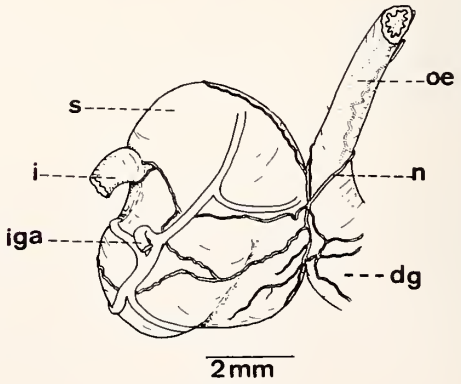


Figure 5

Ventral view of the stomach of *Platydoris argo*. dg, digestive gland; i, intestine; iga, inferior gastric artery; n, nerves; oe, oesophagus; s, stomach.

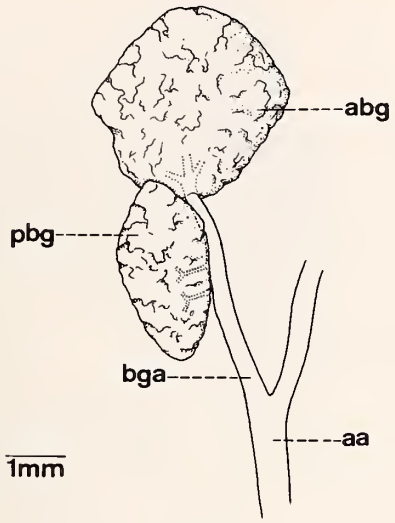


Figure 6

Blood gland of *Platydoris argo*. aa, anterior artery; abg, anterior blood gland; bga, blood gland artery; pbg, posterior blood gland.

branchial ring connects anteriorly with the auricle through the branchiocardiac vein.

Both the afferent and efferent branchial ring are horseshoe-shaped.

## Arterial Circulation

The ventricle lies posterior to a large aortic trunk from which several vessels branch off toward different organs.

The anterior artery (Figure 3, aa) branches anteriorly from the anterior extreme of the aortic trunk (at). At the level of the stomach the inferior gastric artery (Figure 5, iga) branches off and underlies the ventral surface of the stomach. On the right side, at the same level, a branch from the anterior artery passes into the right part of the digestive gland (Figure 3). The anterior artery continues forward, and at the level of the reproductive organs bifurcates, the right branch continuing forward, while the left one passes into the blood glands (blood gland artery, Figure 1, bga). Two small lateral branches connect with the posterior blood gland and then branch throughout that gland. Connections with the anterior blood gland are made

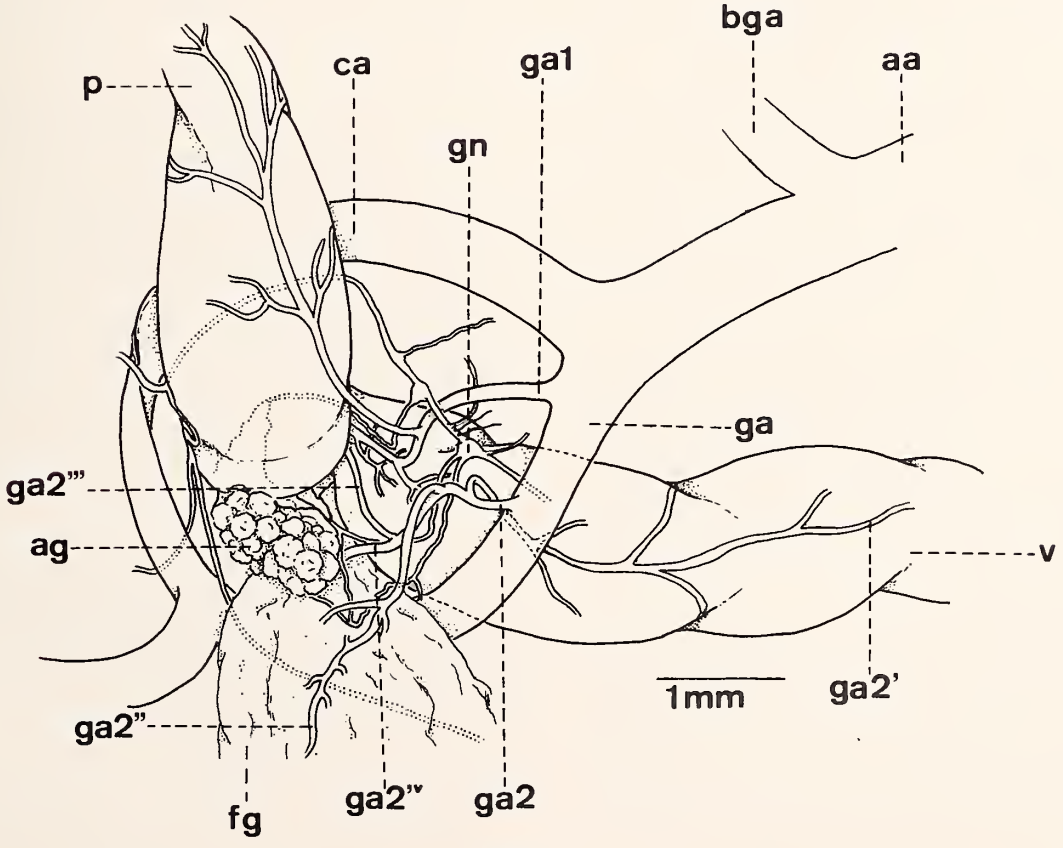


Figure 7

Superior view of the distal part of the genital system of *Platydoris argo*. aa, anterior artery; ag, annex gland; bga, blood gland artery; ca, cephalic artery; fg, female gland; ga, gal, ga2, ga2′–ga2$^{IV}$, genital arteries; gn, genital nerves; p, penis; v, vagina.

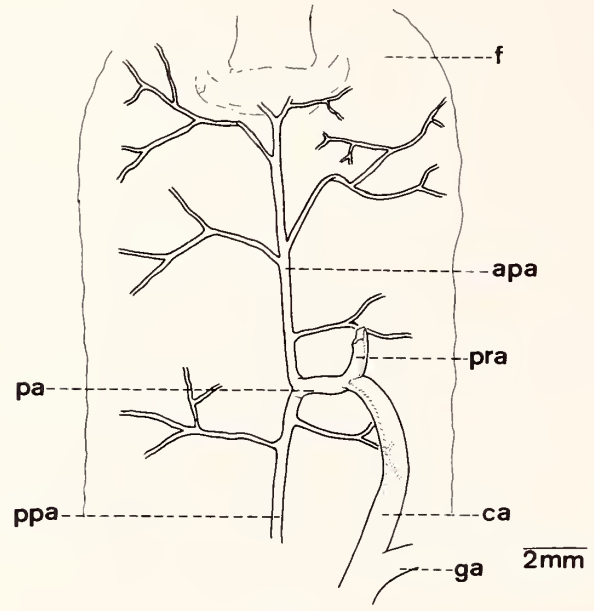


Figure 8

Arterial vessels of the foot of *Platydoris argo*. apa, anterior pedal artery; ca, cephalic artery; f, foot; ga, genital artery; pa, pedal artery; ppa, posterior pedal artery; pra, probuccal artery.

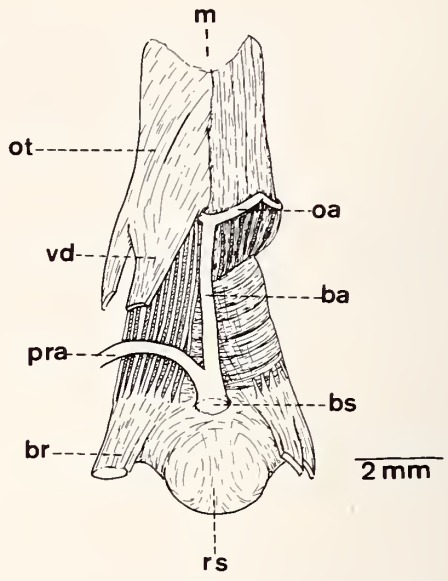


Figure 9

Arterial vessels of the buccal mass (ventral view) of *Platydoris argo*. ba, buccal artery; br, buccal retractor muscle; bs, buccal sinus; m, mouth; oa, oral artery; ot, oral tube; pra, probuccal artery; rs, radular sac; vd, ventrolateral dilator muscle.

through the posterior extreme of the blood gland artery (Figure 6, bga).

The right branch of the anterior artery continues forward and bifurcates again. One branch, the genital artery (Figure 7, ga), extends to the ventral surface of the reproductive organs between the penial and vaginal sheaths; the other, the cephalic artery (ca), continues toward the cephalic region.

The genital artery penetrates the reproductive organs and gives rise to several blood vessels (Figure 7, designated ga1 and subdivisions of ga2). Near the common genital atrium, a side branch of the ga1 extends longitudinally along the penial sac and ramifies. The ga2 gives off several branches to the vagina and outer oviduct (ga2′), female glandular mass (ga2″), common genital atrium (ga2‴) and vestibular gland ($ga2^{IV}$). The genital artery (ga) continues to the female glandular mass.

The cephalic artery (ca) surrounds the penial sac up to the ventral surface of the body and bifurcates; one branch goes to the foot (Figure 8, pedal artery, pa) and the other goes to the buccal apparatus (probuccal artery, pra). The former bifurcates and gives off one branch forward (anterior pedal artery, apa) and another backward (posterior pedal artery, ppa); both vessels are highly ramified.

The probuccal artery enters directly into the buccal apparatus between the buccal retractor muscles (Figure 9, br) and drains into the buccal and odontophoral sinuses. The buccal artery (Figure 9, ba) branches off of the probuccal artery just before it contacts the buccal apparatus. The buccal artery extends forward to the posterior extreme of the oral tube and bifurcates (oral arteries, Figure 9, oa), one branch running to the right and the other to the left on the oral tube (Figure 10).

The superior gastric artery (Figure 3, sga) arises from the aortic trunk, to the left of the anterior artery, and branches of the superior gastric artery supply the oesophagus, stomach, gonad, and digestive gland. Additional blood vessels also supply the gonad, digestive gland, and renal chamber. One of these vessels runs forward and bifurcates (1). The left branch, the prostatic artery, passes to the posterior extreme of the prostate and enters it (pta); the right branch bifurcates, with the two branches passing within the albumen and mucous gland respectively (fga).

### Venous Circulation

Overlying the digestive gland is a large longitudinal sinus (or medial sinus; Figure 3, ms) that receives blood from the veins of the various organs. From the medial sinus blood passes to the afferent branchial ring.

## DISCUSSION

From these detailed observations of *Platydoris argo* the direction of blood flow has been interpreted as follows. Blood from the arterial circulation passes to the pedal arteries and sinuses, which probably contributes to the overall turgor of the foot and provides nutrients and oxygen to the tissues (VOLTZOW, 1985, 1986). From the foot, blood passes to the plexus of sinuses in the notum, which connects

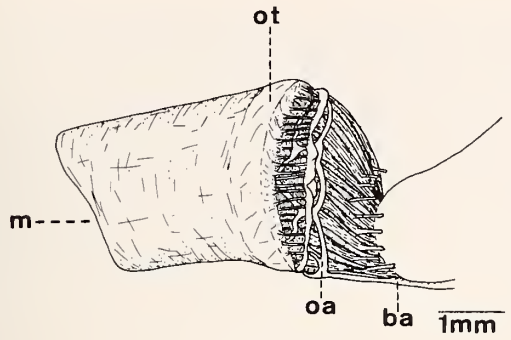


Figure 10

Disposition of the oral artery (lateral view) of *Platydoris argo*. ba, buccal artery; m, mouth; oa, oral artery; ot, oral tube.

to the lateral sinuses. These sinuses drain blood into the auricle through the auricular veins. From the visceral mass, blood flows into the medial sinus and passes backward to the afferent branchial vessels. A similar interpretation was given by HANCOCK & EMBLETON (1852) and ELIOT (1910) for several species of *Doris* and for *Doris tuberculata* Müller, 1778, respectively.

The circulatory system of *Platydoris argo* differs in several ways from that of *Doris* as described by HANCOCK & EMBLETON (1852): (a) the superior gastric artery is independent in *P. argo* (the gastric artery of HANCOCK & EMBLETON [1852] is the inferior artery in *P. argo*); (b) there are only a few connections between the circulatory and excretory systems of *P. argo*, but *Doris* appears to have many; (c) the afferent and efferent branchial rings are horseshoe-shaped in *P. argo*, whereas the rings are closed in *Doris*. ELIOT (1910) found that in *Doris tuberculata* (=*Archidoris tuberculata*) the efferent branchial ring is closed and the afferent branchial vessels are horseshoe-shaped. On the other hand, *Onchidoris bilamellata* Linné, 1767, and *Archidoris pseudoargus* (Rapp, 1827) (see POTTS, 1981) and *Peltodoris atromaculata* Bergh, 1880 (see JONAS, 1985) appear to have afferent and efferent branchial rings similar to those described here for *P. argo*.

The buccal mass circulation of *Platydoris argo* differs fundamentally from that of *Onchidoris bilamellata*, which has been excellently described by CRAMPTON (1977): in *P. argo*, (a) the pedal artery bifurcates into an anterior branch (the anterior pedal artery) and a posterior branch (the posterior pedal artery), both of which extend to the central area of the body; (b) there is only one central buccal artery, which bifurcates into two oral arteries. According to CRAMPTON (1977) in *O. bilamellata* there are two lateral pedal arteries on the right and left side respectively and two buccal arteries.

The circular sinus described in *Platydoris argo* has been noted before in only a few doridaceans: by EVANS (1914) in *Bathydoris browni* Evans, 1914, by MARCUS & MARCUS (1962) in *B. aioca* Marcus & Marcus, 1962, and by MINICHEV (1970) in *B. browni*, *B. obliquata* Odhner, 1934,

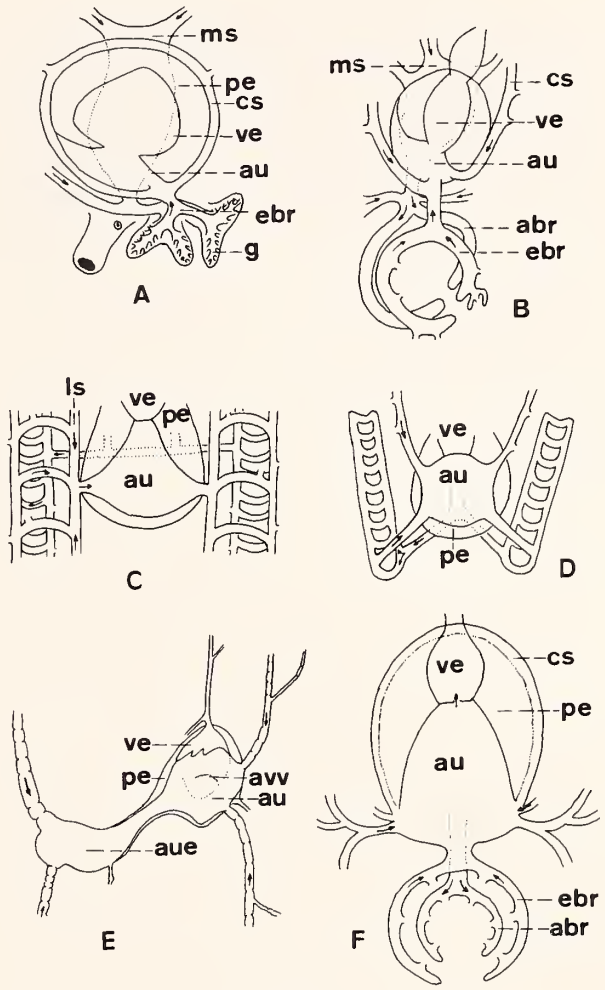


Figure 11

Diagrammatic reconstruction of the venous and branchial regions of Doridacea. A, *Bathydoris obliquata*; B, *B. vitjazi*; C, *Phyllidia pulitzeri*; D, *Corambe*; E, *Doridoeides gardineri*; F, *Platydoris argo* (A and B, after MINICHEV, 1970; C, after WÄGELE, 1984; D, after WÄGELE, 1984, based on FISCHER, 1892; E, after ELIOT & EVANS, 1908). The arrows represent the direction of blood flow. abr, afferent branchial ring; au, auricle; avv, auriculoventricular valve; cs, circular sinus; ebr, efferent branchial ring; g, gill; ls, lateral sinus; ms, medial sinus; pe, pericardium; ve, ventricle.

and *B. vitjazi* Minichev, 1969. However, in these species the circular sinus opens to the plexus of sinuses from the peripheral circulation, before connecting to the auricle (Figure 11A, B). We have not seen such openings in *P. argo*. On the other hand, in the most primitive species of the genus *Bathydoris* (*i.e.*, *B. browni*, *B. obliquata*), the circular sinus surrounds the pericardium (Figure 11A), whereas in higher species (*i.e.*, *B. vitjazi*), the circular sinus has a tendency to become separated from the pericardium to form the lateral sinuses that are present in the majority of Doridacea (Figure 11B). Thus, in *P. argo*, which has well-differentiated lateral sinuses, the circular sinus could